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THE JUNCAGINACEAE IN THE SOUTHEASTERN UNITED STATES¹

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JUNCAGINACEAE L. C. Richard, *Démonstr. Bot.* ix. 1808, "Juncagines,"
nom. cons.

(ARROWGRASS FAMILY)

Perennial [or annual], glabrous, typically perfect-flowered [dioecious], scape herbs, the axis sympodially branched, bulbous or rhizomatous, sometimes with runners, often covered with old leaf bases, the roots fibrous [sometimes tuberiferous]; starch grains of pteridophyte type. Leaves basal, alternate, distichous or spirodistichous, sessile, linear to almost filiform [filiform], terete to semiterete [dorsiventrally or laterally flattened (i.e., ensiform)], ligulate [cligulate]; axillary scales (squamules) present; stomata mostly paracytic. Inflores-

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cence of terminal, bractless, pedunculate racemes [spikes] [rarely reduced to a single terminal flower]. Flowers actinomorphic to zygomorphic, hypogynous, perfect to imperfect, anemophilous, proterogynous. Perianth of 6 [4] (or fewer by abortion) distinct and mostly similar tepals in 2 whorls. Androecium usually of 6 [4] subsessile stamens (or fewer by abortion) in 2 whorls, each filament adnate at its base to the base of the subtending tepal; anthers tetrasporangiate, bilocular at anthesis, extrorse, opening by lengthwise slits, the tapetum ameboid, microsporogenesis of the successive type; pollen grains globose to ellipsoid, monocolpate, inaperturate, binucleate (sometimes trinucleate?) when shed. Gynoeceum of 6 [4] carpels in 2 whorls (occasional flowers with 3 to 12 carpels), these more or less adnate to the central axis (carpophore) [or central axis lacking], some commonly sterile, the fertile carpels eventually separating from the axis [the carpels connate at least basally, forming a compound ovary in *Maundia* and *Tetroncium*]; styles short to lacking [well developed, subulate, and persistent as beaks on the fruit in *Tetroncium*]; stigmas distinct, plumose to papillose; ovary 1-locular [2-4-locular in *Maundia*, incompletely 4-locular in *Tetroncium*], each locule with a single ovule, this bitegmic, crassinucellar, anatropous [orthotropous], and erect [pendulous in *Maundia*]; megagametophyte (embryo sac) development of the Polygonum (normal) type; endosperm development nuclear; embryogeny of the caryophyllad type. Fruit schizocarpic, the mericarps indehiscent, achenelike [fruit essentially capsular(?) in *Maundia* and *Tetroncium*]; seed linear to ovoid, without endosperm [this present in *Tetroncium*], the embryo straight. (Excluding *Lilacaceae* Dumortier, 1829, and *Scheuchzeriaceae* Rudolphi, 1830, nomina conservanda.) TYPE GENUS: *Juncago* Séguier, nom. illeg. = *Triglochin* L.

A small family of three genera and about 22 species: the monotypic *Maundia* F. Mueller (*M. triglochinoides* F. Mueller), of coastal eastern Australia (New South Wales and Queensland); the likewise monotypic *Tetroncium* Willd. (*T. magellanicum* Willd.), of the Falkland Islands and southern South America (from Tierra del Fuego, northward in the Andes to at least 40°S in Argentina and Chile), unique in the family because it is dioecious; and the widely distributed *Triglochin* L. (including the Australian *Cynogeton* Endl.), about 20 species, one of which occurs in the southeastern United States.

The circumscription of the Juncaginaceae here accepted (with three genera) has ample precedent in the literature (e.g., by Chant; Cook; Engler & Diels; Hutchinson; Kimura; Mason; Tomlinson, 1982), but the relationships of two additional genera, *Scheuchzeria* L. and *Lilaea* Humb. & Bonpl., remain unsettled. Both (e.g., by Agrawal; Britton; Buchenau, 1903; Buchenau & Hieronymus; Hegi; Johri; Lotsy; Rendle; Suessenguth; Thorne, 1976, 1983; and Wettstein) or either one of these (*Scheuchzeria* only, by authors including Abrams; or *Lilaea* only, by those including Cronquist, 1968, 1981; Dahlgren & Clifford; Dahlgren, Clifford, & Yeo; Markgraf, 1981; Eckardt; Stebbins; and Takhtajan) may be included in an amplified version of the Juncaginaceae.

That *Scheuchzeria* represents a family by itself is accepted by the majority of workers after 1940 (see summary of the various monocot systems in Dahlgren & Clifford). Among the "large" number of important features (Tomlinson,

1982) in which this genus differs from *Triglochin* and *Lilaea* are three- (vs. two-)celled pollen; bioovulate (vs. uniovulate) carpels; helobial (vs. free-nuclear) endosperm; the presence (vs. absence) of hypodermal crystals, a leaf apical pore, and floral bracts; and the absence (vs. presence) of squamules (minute scale- or gland-like outgrowths occurring in the axils of leaves; unique in the Helobiae). Floral developmental evidence further confirms the separate familial status of *Scheuchzeria* (Posluszny). A character common to all three genera, however, is the occurrence of the cyanogenic glucoside triglochinin.

The placement of *Lilaea* appears to be less certain. With *Triglochin* it shares two-celled pollen, uniovulate carpels, free-nuclear endosperm, and squamules. Both genera have an unusual type of embryo development in which the "first embryonic root does not originate from the point where the suspensor is attached, but from the lateral position . . . directly from the epidermis of the embryo, therefore not in the manner of adventitious roots, which develop from the deep inner tissue" (Yamashita, p. 205). *Lilaea* differs from *Triglochin* in the number of carpels (one vs. six) and perianth segments (one vs. six) and in the presence of laticifers (also lacking in *Scheuchzeria*). Tomlinson (1982), whose discussion of the three genera is outstanding, concluded that it is better to retain the separate familial status of *Lilaea* until a more extensive study has been made. (See also Posluszny *et al.* and Singh.) It should be noted that knowledge of Juncaginaceae (*sensu stricto*) is based mostly on Northern Hemisphere representatives of the family; more data are needed on species of *Triglochin* of the Southern Hemisphere, especially those of Australia, most of which are diminutive annuals, as well as on *Tetroncium* and *Maundia*.

Many authors accept a close relationship between the Juncaginaceae and the Potamogetonaceae. Takhtajan suggested that the latter may well be derived from the former (and that the Posidoniaceae probably represent an extreme marine stage of the Juncaginaceae). (Engler & Diels and Skottsberg even included the Juncaginaceae in the Potamogetonaceae.) Such a relationship was postulated over a century ago by Bentham (p. 165): "*Triglochin* . . . appears to me to be much more nearly connected with *Potamogeton* [than with *Alismaceae*], in the peculiar structure of the flowers, differing chiefly in habit, and even in that respect, the half-floating leaves of *T. procera* show a near approach to that genus." Hutchinson (p. 678) expressed the opinion that "the primitive tribe Helonieae of the Liliaceae has been developed from the same stock as the Juncaginaceae; the general facies of its genera is the same and in both groups the flowers are quite ebracteate." Joseph D. Hooker pointed out that the habit of *Tetroncium* is precisely that of *Nartheceum* of the Liliaceae.

Fruit types in the family have been variously, and often questionably, denominated and described. I find, for example, no convincing evidence that the fruits of any of the three genera are indeed "follicles" or that they are "dehiscent." The fruits of *Triglochin* appear to me to be schizocarpic, the mericarps indehiscent (see under *Triglochin* below). Those of the other genera are essentially capsular according to some authors: in *Maundia*, "carpels 2-4, united along the whole length of their inner faces. Fruiting carpels . . . remaining united and together forming a 2- to 4-angled squat cylinder truncate at the summit with 2-4 short spreading beaks" (Aston, p. 241); and in *Tetroncium*, "carpels

4, united at base into incompletely 4-locular ovary. . . . Fruit indehiscent, 4-celled, seed usually single, with three aborted ovules" (Moore, 1968, p. 137). Both genera were included among those with capsular fruits by Dahlgren & Clifford, but three years later Dahlgren, Clifford, & Yeo (p. 312) wrote of them: "carpels . . . more or less fused centrally . . . but becoming separate in the fruit stage." Bentham (p. 169) described the carpels of *Maundia* as being "almost drupaceous, each with a thinly cartilaginous endocarp." According to Thompson (p. 80), the "fruiting carpels [are] joined at the adaxial angle [and have] a spongy covering on the ventral surface." Developmental study of the fruits of both *Maundia* and *Tetroncium* is called for.

Although seeds of the Juncaginaceae are usually described as lacking endosperm, *Tetroncium* is apparently an exception. Of this genus J. D. Hooker (p. 359) wrote "albumen farinaceum." Buchenau (1882, p. 472) acknowledged this exception in a footnote to his assertion that "Der Samen der Juncaginaceen enthält bekanntlich kein Albumen." Later, however, he and Hieronymus (p. 223) were skeptical ("*Tetroncium* mit kleinem Nährgewebe?"). Finally, however, Buchenau (1903, pp. 2, 6), apparently on the basis of his own observation, agreed with J. D. Hooker: "Embryo . . . in *Tetroncio* albuminosus" and "Nur bei *Tetroncium* liegt der . . . Embryo . . . in einem stärkemehlreichen Nährgewebe."

Noteworthy anatomical features of the Juncaginaceae include a single ring of collateral vascular bundles in the inflorescence axis, imparting an "exceedingly dicotyledonous" look (Chrysler, p. 180); the reported occurrence of an "incipient cambium" in the rhizome bundles (Andersson, Hill, Salisbury) (" . . . perhaps . . . a case of incipient secondary thickening which is found developed to a much greater extent in Monocotyledons like *Aristea*, *Dracaena*, *Yucca*, etc."; Hill, p. 88); the presence of so-called axillary squamules, which are of wide occurrence in the Alismatidae (and one species of Araceae) (Arber [1923] considered them as appendages originating from the abaxial epidermis of the leaf just distal to the leaf in the axil of which they are found); and inflorescence formation by apical bifurcation of the axis (the original terminal meristem forming the inflorescence, the axillary bud of the distalmost leaf continuing further vegetative growth; reported in other Alismatidae).

Adoption of the name Scheuchzeriaceae (e.g., by Kartesz & Kartesz) when *Scheuchzeria* and *Triglochin* are included in the same family is incorrect. The name Juncaginaceae predates Scheuchzeriaceae by 22 years. If the Juncaginaceae are merged with the Potamogetonaceae Dumort. (1829), the latter name must be used (see International Code of Botanical Nomenclature, 1983, Appendix II).

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1. *Triglochin* Linnaeus, Sp. Pl. 1: 338. 1753; Gen. Pl. ed 5. 157. 1754.³

Perennial [annual], perfect-flowered, herbaceous plants of wetlands, axis sympodially branched, somewhat [to strongly] bulbous [rhizomatous], with [without] runners, the roots fibrous [sometimes tuberiferous]; vessels confined to the roots. Leaves basal, distichous, sessile, linear, terete or semiterete [flat], ligulate [eligulate], sheathing, the sheath open. Inflorescence of terminal, bractless, pedunculate racemes [spikes] [rarely reduced to a single terminal flower]. Flowers actinomorphic, perfect to imperfect. Perianth of 6 tepals (or fewer by abortion) in 2 whorls, the upper whorl seemingly distal to the lower whorl of stamens. Androecium of 6 subsessile stamens (or fewer by abortion) in 2 whorls, each filament adnate at its base to the base of the subtending tepal, the stamen and tepal typically deciduous as a unit; pollen inaperturate, spheroidal, reticulate, binucleate (sometimes trinucleate?) when shed. Gynoecium of 6 carpels (occasional flowers with 3 to 12), these more or less adnate to the prolonged central axis (carpophore) [or central axis not prolonged, the carpels free], the lower 3 usually sterile, remaining attached to the axis as wings or ridges, the upper 3 [or all 6] eventually separating from the axis; styles short or lacking; stigmas distinct, plumose to papillose. Fruit schizocarpic, the mericarps indehiscent, achenelike [gynoecium apocarpous, the carpels achenelike in *T. procerum*]. TYPE SPECIES: *T. palustre* L.; see N. L. Britton, N. Am. Fl. 17: 41. 1909. (Name from Greek *treis*, three, and *glochis*, point, from the pointed carpel bases of *T. palustre*, which spread from the axis at fruit maturity, the gynoecium then slightly recalling a three-barbed spear-point.)—ARROWGRASS.

A genus of about 20 species in two subgenera, widely distributed but best represented in the Southern Hemisphere, especially in Australia. Subgenus CYCNOGETON (Endl.) Buch. (characterized by perennial habit, free carpels, and lack of a carpophore) embraces a single species, *Triglochin procerum* R. Br., which occurs in southern New Guinea and Australia (including Tasmania).

³The name *Triglochin* has been—and continues to be—treated as feminine by many authors, either because *glochis* is a feminine noun or, more likely, because others do it that way. Linnaeus, however, used the name as neuter, and his choice should be followed (ICBN, 1983, Rec. 75A. 3).

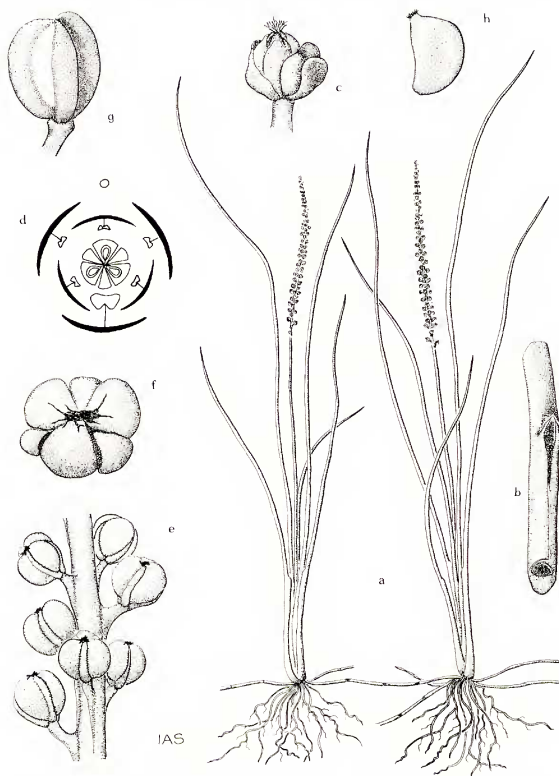


FIGURE 1. *Triglochin*. a-h, *T. striatum*: a, habit, $\times \frac{1}{2}$; b, portion of leaf sheath to show ligule, $\times 4$; c, flower, the fertile stamen and its subtending tepal to the right, $\times 12$; d, floral diagram (after Lieu), showing 6 tepals (5 with sterile stamens), 3 sterile and 3 fertile carpels, the latter each with a single 2-integumented ovule; e, portion of infructescence, $\times 6$; f, mature fruit with 3 fertile and 3 sterile carpels, from above, $\times 12$; g, persistent sterile carpels after removal of fertile mericarps, $\times 12$; h, fertile mericarp, $\times 12$.

Triglochin procerum var. *dubium* (R. Br.) Benthams is recognized by some (e.g., Cunningham *et al.*) as a distinct species. *Triglochin procerum*, water-ribbons, is the most aquatic of its congeners, with its leaves up to 2(–3.5) m long (Aston) when the plant grows in deep, flowing water, the distal portion floating or the entire leaf submersed and trailing downstream (in the manner of *Sparganium* L. or *Vallisneria* L.).

Subgenus TRIGLOCHIN (characterized by annual or perennial habit and—except in one annual—the adnation of carpels to a carpophore) is found on all continents except Antarctica. The single species of the southeastern United States, *Triglochin striatum* Ruiz & Pavon (*T. floridanum* Gand., *T. sessile* Gand., *T. triandrum* Michaux) is one of several species (number uncertain; see below) of its genus in North America. In our area it occurs along the coast from Maryland to Louisiana, typically in brackish and saline habitats (marshes, meadows, ditches, swamps), often in shallow water. An impressively wide-ranging plant, it is also distributed in the western United States (Oregon and California), the Valley of Mexico, the Bahamas, Cuba, South America (Peru and southeastern Brazil south to Tierra del Fuego), southern Africa (Cape Peninsula to Angola and Mozambique), and other extratropical regions, mostly coastal Australia (Western Australia to Tasmania and southeastern Queensland), New Zealand, and the Auckland and Chatham islands.

The taxonomy of *Triglochin*, at least in North America, is unsettled; estimates of the number of species here range from three (e.g., Britton) to six (e.g., Kartesz & Kartesz). The circumboreal *T. maritimum* complex, source of most of the uncertainty, is in need of critical study worldwide (see Löve & Löve, 1958a). The North American species of *Triglochin*, all perennials, typically grow in brackish, saline, and alkaline hydric habitats (less frequently in fresh water), especially in the western United States and western Canada, and to the north of our area.

The flowers of *Triglochin* have one or two whorls of three “bractiform perianth-like appendages” (Mason, p. 95), the nature of which has been much discussed. Each appendage subtends and is adnate at its base to a stamen (these reduced in some species), the two typically falling as a unit. The upper whorl of appendages appears to diverge from the axis *above* the lower whorl of stamens; its vascular supply, too, arises *above* that of the lower stamens (Uhl). This morphology led Uhl to interpret the flower of *Triglochin* as a reduced inflorescence of six staminate flowers and one or more naked carpellate flowers, each carpel probably representing a single flower (see also Burger). Such an interpretation has been questioned by Lieu, who found (p. 1418) that both whorls of tepals are initiated in acropetal succession *before* initiation of the stamens, that the anomalous position of the upper tepals results from “differential timing and rates of growth of the inner tepals and outer stamens,” and that “the evidence does not support the interpretation of the flower of *Triglochin* as a reduced lateral branch of [an] inflorescence.” Lieu did note that emphasis on vasculature would support interpretation of the flower as an inflorescence, but that developmental studies refute such an interpretation and lend support to regarding the flower of *Triglochin* as comparable to the ordinary trimerous monocotyledonous flower.

The flowers of those perennial species for which the floral biology has been studied (*Triglochin maritimum*, *T. palustre*, and *T. striatum*) are proterogynous, the penicillate stigmas protruding from the perianth two to three days before stamen maturation. Anthers of the lower whorl of stamens dehisce after the stigmas have turned brown, their pollen falling not onto the stigmas of that flower but into the deeply concave tepal below each stamen. The wind finally carries the pollen away or shakes it onto more proximal flowers. The stamens, each often attached to its tepal, eventually drop off. This sequence of events is then repeated for the upper whorl of stamens. Pollen deposition on stigmas of the same flower was reported for the Australian annuals studied by Keighery. These species and at least *T. maritimum*, *T. palustre*, and *T. striatum* are autogamous and show no significant difference in seed set between open pollination and enforced selfing. In contrast, *T. gaspense* Lieth & Löve, when grown in a greenhouse, did not set seed except when pollinated by hand (Löve & Lieth).

Carpel number in *Triglochin*, although variable, is usually six (but as few as three and as many as 12 have been observed in occasional flowers). In some species (e.g., *T. maritimum*) all six carpels are fertile, eventually falling as achenelike mericarps from the persistent and terete or merely angled carpophore. In others (e.g., *T. palustre*, *T. striatum*) the three carpels of the outer whorl are sterile (even vestigial) and remain adnate to the thereby winged or ridged carpophore after the inner, fertile carpels have fallen; they often then assume "the appearance of dissepiments of a capsule" (Bailey, 1902, p. 1705). Of the species in subg. TRIGLOCHIN, only *T. turrifera* Ewart, one of the Australian annuals, is said to lack a carpophore.

Chromosome counts, some undocumented, have been published for about ten species of *Triglochin*. *Triglochin procerum* (subg. CYCNOGETON) has diploid, tetraploid, and octoploid "morphological forms" ($2n = 16, 32, 64$; Robb & Ladiges).

In subg. TRIGLOCHIN the most counted taxon is *Triglochin maritimum* agg., for which seven out of 12 possible numbers in a polyploid series from diploid (12) to 24-ploid (144) have been noted, some from the Old World, some from the New. (Not fitting into this series are counts of $2n = 30$ [Bolkhovskikh *et al.*] and 56 [Looman] in *T. maritimum*, or $n = 75-77$ [Gervais & Cayouette] in *T. elatum* Nutt., a member of the *T. maritimum* aggregate.) According to Löve & Löve (1958a, p. 20), *T. maritimum* is "one of the most collective species known and so heterogeneous that its inclusion in the so-called circumpolar element of distribution is highly misleading." They (1958b, p. 162) further stated that this "supposedly circumpolar [taxon] is in fact an aggregate of at least more than a dozen good species."

Counts for *Triglochin palustre*, which shares with *T. maritimum* a distribution in both the Old and New worlds, are $2n = 12, 18, 24, 26, 28, 36, 48$; perhaps this taxon, too, is an aggregate (Hess *et al.*).

A strictly North American taxon for which a count is available is *Triglochin gaspense*, $2n = 96$. Counts for Old World taxa include *T. Barrelieri* Loisel., $2n = 30$; *T. bulbosum* L., $2n = 18$; and *T. laxiflorum* Guss., $2n = 18$. I know of no counts for either *T. striatum* or any of the Australian annuals.

Dispersal of species of *Triglochin* needs further study. Some are certainly hydrochorous. *Triglochin procerum* has been seen to drop its disseminules into the water of a stream, where they were carried away (Keighery). Pojar observed floating seedlings of *T. maritimum*, and mericarps of this species have been collected from drift-line debris (Boorman). However, "seeds" of *T. maritimum* (and of *T. palustre*) float for less than a week in fresh water (perhaps a bit longer in salt water), according to Praeger. Epizoochory in mud and anemochory have been suggested for *T. maritimum* (Pojar).

Disseminules of species of *Triglochin* with mucronate, spurred, or even hooked apices or bases (e.g., *T. palustre* and some of the Australian annuals) have been assumed to be epizoochorous by attachment, an assumption that requires verification. Animal dispersal of the Australian annuals has been questioned by Keighery, who found that in these plants, which occupy shallow, sandy, winter-wet depressions, seed dispersal "has been reduced to a minimum . . . ensuring that the species will occupy the same favourable area next year" (p. 83). It seems possible that in these annuals the structural devices that seem to fit them for animal dispersal serve rather as "anchors" in favorable habitats.

Triglochin maritimum and *T. palustre*, considered in some regions to be "fairly" good forage, may be relished by livestock because of the salt content of the leaves. In the western United States and western Canada, however, both species (but especially *T. maritimum*) are among the major plants poisonous to cattle and sheep, the toxic principle being hydrocyanic acid. Death results from asphyxia or, in severe cases, respiratory failure. *Triglochin striatum* seems not to have been implicated in poisoning; it is grazed by sheep in Chile (Alduante *et al.*) and is considered a good salt-marsh fodder in Australia (Bailey, 1883).

Species of *Triglochin* may be of importance as food for wildlife in some regions. At James Bay, Canada, for example, the perennating bulbs of *T. palustre* were found to be the most strongly selected food item of snow geese (Prevett *et al.*).

The young leaves of *Triglochin maritimum*—their dubious qualities notwithstanding—can be cooked and eaten as a vegetable. They emit an unpleasant odor when cooking ("an Chlor erinnerende"; Suessenguth, 1935, p. 214) and are reputed to be a "blood-purifier." Ashes from this species are rich in sodium carbonate and can be used in making soap (Fedchenko). The fruits were parched and eaten by Oregon's Klamath Indians, who also roasted them as a substitute for coffee (Coville). *Triglochin procerum* produces globose root tubers 2–3 cm across (Van Steenis), of which Mueller (1867–1868, p. 83) said, "tubera edulia nativis avide quaesita."

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